An Experimental Test of Darwin's Naturalization Hypothesis

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ABSTRACT: One of the oldest ideas in invasion biology, known as Darwin's naturalization hypothesis, suggests that introduced species are more successful in communities in which their close relatives are absent. We conducted the first experimental test of this hypothesis in laboratory bacterial communities varying in phylogenetic relatedness between resident and invading species with and without a protist bacterivore. As predicted, invasion success increased with phylogenetic distance between the invading and the resident bacterial species in both the presence and the absence of protistan bacterivory. The frequency of successful invader establishment was best explained by average phylogenetic distance between the invader and all resident species, possibly indicating limitation by the availability of the unexploited niche (i.e., organic substances in the medium capable of supporting the invader growth); invader abundance was best explained by phylogenetic distance between the invader and its nearest resident relative, possibly indicating limitation by the availability of the unexploited optimal niche (i.e., the subset of organic substances supporting the best invader growth). These results were largely driven by one resident bacterium (a subspecies of *Serratia marcescens*) posting the strongest resistance to the alien bacterium (another subspecies of *S. marcescens*). Overall, our findings support phylogenetic relatedness as a useful predictor of species invasion success.

Keywords: bacteria, biological invasions, competition, Darwin's naturalization hypothesis, microbial microcosms, phylogenetic relatedness.

Introduction

What makes some nonnative species successful invaders of communities to which they have been introduced? Our ability to answer this question is key for designing effective means to mitigate widespread biological invasions that have profoundly changed the world's many ecosystems (Vitousek et al. 1996; Mack et al. 2000) and have incurred considerable economic loss (Pimentel et al. 2005). Traditionally, this question has been tackled from two largely disparate perspectives, with one aiming to identify species-level traits shared by successful invaders (Rejmanek 1996; Rejmanek and Richardson 1996; Kolar and Lodge 2001) and the other searching for attributes of communities that influence their invasibility (Rejmanek 1989; Levine and D'Antonio 1999; Davis et al. 2000). The considerable amount of work conducted within each framework so far, however, has yielded few generalizations (Colautti et al. 2006; Moles et al. 2008). The lack of predictive power of either approach has led to the proposition that our ability to predict invasion success may be enhanced by considering the traits of invading species and resident communities together (e.g., Lodge 1993; Moles et al. 2008).

One idea that falls within the above proposition is Darwin's naturalization hypothesis, which posits that naturalization of nonnative species is more likely in communities in which their close relatives are absent (Darwin 1859). This hypothesis arose from a related hypothesis of Darwin (1859) that closely related species tend to possess similar niches and hence perform similarly under the same environmental conditions (for a recent empirical example, see Brandt et al. 2009), translating into strong competition imposed by resident species on closely related invaders that reduces their success. These two hypotheses serve as the conceptual base of contemporary phylogenetic community ecology: whether co-occurring species exhibit phylogenetic overdispersion (i.e., being less phylogenetically related than expected by chance), as implied by the former hypothesis, and whether species niche is phylogenetically conserved, as suggested by the latter hypothesis, have been major topics of this research field (reviewed in Webb et al. 2002; Cavender-Bares et al. 2009). Within this context, there have been multiple attempts at testing Darwin's naturalization hypothesis (reviewed in Proches et al. 2008). Together, these studies have reported positive (Daehler 2001; Duncan and Williams 2002), negative (Mack 1996; Rejmanek 1996, 1998; Strauss et al. 2006), or no (Lambdon and Hulme 2006; Ricciardi and Mottiar 2006) relationships between naturalization of introduced species and their relatedness to native communities. These mixed results parallel those in studies of phylogenetic community structure that have revealed various patterns of phylogenetic dispersion (summarized in Cavender-Bares et al. 2009). Strictly speaking, however, none of these studies can be considered rigorous tests of Darwin's naturalization

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We used simple and backward-selection multiple logistic regressions to model the frequency of successful establishment of the invader as a function of realized nearest phylogenetic distance, average phylogenetic distance, and resident species richness. We included resident species richness as a predictor variable in the regressions because it has frequently been linked to invasion success (Fridley et al. 2007). We viewed the invader establishment as successful if it attained above-zero density (results remained the same when using the lowest positive invader density as the threshold). Realized resident species richness of each treatment was calculated as the average number of species found in the three replicates destructively sampled before invasion; the averaging was necessary because it prevented the arbitrary assignment of measured species richness values (if different between replicates) to the remaining three replicates to which the invader was introduced. Realized nearest and average phylogenetic distances were calculated similarly. We used simple and backward-selection multiple linear regressions to model invader population density as a function of the same three predictor variables. Before performing multiple regressions, we discarded data from communities that contained only a single resident species before invasion, since average and nearest phylogenetic distances were equal in these communities, confounding the analyses. Simple linear regression was also used to assess the relationship between invader-resident phylogenetic distance and trait distance. In all regressions, explanatory variables were deemed significant if $P \leq .05$ and marginally significant if $.05 < P \leq .10$; explanatory variables were retained in multiple regressions only if $P \leq .05$. Analyses were done for the control and predation treatments separately. Data on invader population density were $\log_{10}$ transformed ($\log_{10}(x + 1)$) to reduce heteroscedasity and improve normality. All analyses were conducted in SAS 9.1 (SAS Institute, Cary, NC).

Results

In the predator-free controls, the invader successfully established in all but three microcosms. Presumably because of this low failure rate, the frequency of successful invader establishment only marginally increased with average phylogenetic distance and was unaffected by nearest phylogenetic distance or species richness (table 1). A multiple logistic regression eliminated all three explanatory variables as significant predictors of invader establishment. Invader population density was also unaffected by species richness (fig. 2; $R^2 = 0.004$, $P = .6791$) but increased with nearest (fig. 2; $R^2 = 0.429$, $P < .0001$) and average (fig. 2; $R^2 = 0.408$, $P < .0001$) phylogenetic distances. Nearest phylogenetic distance was the only variable retained in the multiple regression that best explained invader density.

Similar results emerged in the predation treatment, where the invader successfully established in fewer (26 out of 45) microcosms. The frequency of successful establishment increased significantly with increasing average phylogenetic distance but was again unaffected by nearest phylogenetic distance or species richness (table 2). A multiple logistic regression retained average phylogenetic distance as the only significant predictor of invader establishment. Invader population density was again unaffected by species richness (fig. 2; $R^2 = 0.013$, $P = .4561$) and increased with nearest (fig. 2; $R^2 = 0.764$, $P < .0001$) and average (fig. 2; $R^2 = 0.594$, $P < .0001$) phylogenetic distances. Nearest phylogenetic distance was again the only significant variable retained in a multiple regression that explained invader density.

There was a significant positive relationship between invader-resident phylogenetic distance and trait distance ($R^2 = 0.9997$, $P = .0114$), indicating that carbon use patterns of these bacteria are phylogenetically conserved.

Discussion

Darwin's naturalization hypothesis emphasizes the importance of the relatedness between invading and resident species in determining invasion success at the scale of species interactions. Observations of exotic species in various regions larger than this scale have provided mixed support for this hypothesis (Mack 1996; Rejmanek 1996, 1998; Daehler 2001; Duncan and Williams 2002; Lambdon and Hulme 2006; Ricciardi and Mottiar 2006; Strauss et al. 2006). In particular, Diez et al. (2008) have shown that the relationship between the abundance of exotic plant species and that of their native congeners changed from positive at the regional scale of Auckland, New Zealand, to negative at the scale of ecosystems within the region; however, the latter scale is still considerably larger than the scale that species normally interact. Here, we took a direct approach in examining the hypothesis by experimentally manipulating phylogenetic relatedness between invading species and resident communities in small-scale laboratory microcosms. In support of the hypothesis, our results showed that invaders were more successful when they were more distantly related to resident species in both the presence and the absence of predators. Also as envisioned by Darwin (1859), we showed that resident species more closely related to the invader shared more similar traits with the invader.

Somewhat surprisingly, neither invader establishment nor abundance was a significant function of resident species richness. This result is at odds with another classic idea in invasion biology stating that diverse communities are better at resisting invasion than their depauperate counterparts (Elton 1958), which has so far received abun-

Table 1: Results of separate logistic regressions on invader establishment in the control (no predation) treatment

Source	df	χ^2	P	95% odds ratio confidence interval
Average phylogenetic distance	1	2.9762	.0845	.047, >999.99
Nearest phylogenetic distance	1	.0033	.9541	<.001, >999.99
Resident species richness	1	1.8948	.1687	.396, 200.863

dant experimental support (Levine et al. 2002; Fridley et al. 2007). Note that the opposite diversity-invasibility pattern has often been found in observation studies of natural communities, which has largely been attributed to the operation of larger-scale mechanisms associated with spatial heterogeneity (sensu Fridley et al. 2007). The principal explanation for the negative diversity-invasibility relationship in diversity-manipulation experiments is that diverse communities offer greater biotic resistance through more resource use, leaving less resource available for invaders. Our results, however, suggest that species richness may not always be a good indicator of resource use that is most relevant for invading species. The positive relationship between phylogenetic distance and invasion success found in our experiment, coupled with the observed phylogenetic niche conservatism, suggests that competition from closely related resident species most effectively suppressed invading species by virtue of sharing similar resources, just as envisioned by Darwin (1859). Here resident species richness failed to capture this important role of phylogenetic relatedness and trait similarity in regulating invasion success, as indicated by its lack of relationship with average ($R^2 = 0.052$, $P = .1326$ in the controls and $R^2 = 0.073$, $P = .0730$ in the predation treatment) and nearest ($R^2 = 0.015$, $P = .4292$ in the controls and $R^2 = 0.051$, $P = .1351$ in the predation treatment) phylogenetic distances. We recognize that our relatively small diversity gradient, with the highest richness level lower than that of the majority of natural communities, and the resultant small phylogenetic gradient likely placed a constraint on these relationships. It is possible that resident species richness and phylogenetic relatedness are more strongly related in experiments encompassing broader diversity ranges, given the simple scenario that increasing species richness by chance alone increases the likelihood of including resident species that are closely related to the invading species (essentially a sampling effect [sensu Tilman et al. 1997] for closely related species). Reanalyzing data from previous diversity-invasibility experiments using a phylogenetic approach will be able to test this hypothesis.

We found that average and nearest phylogenetic distances between the invader and resident communities best explained invader establishment and abundance, respectively. The two phylogenetic distances provide complementary information on the relatedness of invading and resident species (Strauss et al. 2006): whereas average distance is indicative of the distinctness of the invading species relative to the entire resident community, nearest distance is a surrogate of niche differences between the invading species and its closest resident relative (with the assumption of phylogenetic niche conservatism). As such, one would expect that resident communities with smaller average phylogenetic distances from the invading species have a smaller unoccupied niche left for the species, resulting in its lower establishment success. On the other hand, one should also expect that after becoming established, invaders would attain small abundance if their optimal niche has already been occupied by their closely related resident species. In our experimental microcosms with continuous shaking (i.e., little opportunity for spatial niches), the diverse organic substances in the medium that can be used by the invader may constitute its niche, whereas the subset of substances that support the best growth of the invader may constitute its optimal niche. The positive relationship between average phylogenetic distance and invader establishment thus suggests that the availability of the unexploited niche may have limited the successful settlement of the invader. The positive relationship between nearest phylogenetic distance and invader abundance suggests that the availability of the unexploited optimal niche may have limited the abundance of the invader. Together, these findings support the proposition that mechanisms regulating invasion success may differ between the establishment and spread stage of invasions (e.g., Kolar and Lodge 2001; Duncan et al. 2003; Diez et al. 2008). Note that at first sight, our results do not agree with those of Strauss et al. (2006), who found that the invasiveness of introduced grasses in California was better explained by average phylogenetic distance. The analyses of Strauss et al. (2006), however, were based on categorical classification of species invasiveness, that is, whether introduced species have become widespread (invasive species) or not (noninvasive species). It remains to be seen whether their results would change if actual species abundance data were used. The robustness of our results, of course, also needs to be evaluated in other systems.

It should be noted that the invader and one resident species in our experiment represent two subspecies of the

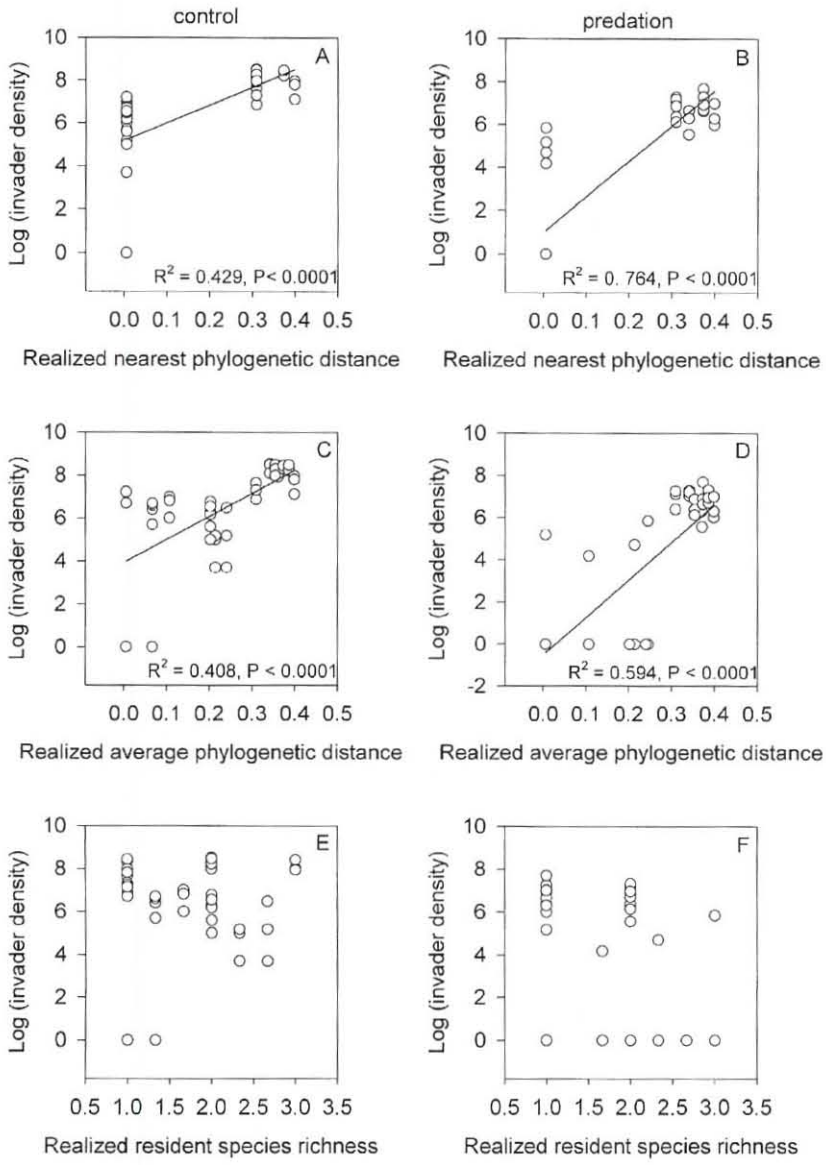

Figure 2: Relationship between realized nearest phylogenetic distance (*A*, *B*), realized average phylogenetic distance (*C*, *D*), and realized resident species richness (*E*, *F*) and invader population density in the control (*left column*) and predation (*right column*) treatments. Data are shown along with linear regression lines (if significant). Log-transformed invader density was originally measured as the number of colony-forming units per milliliter.

same bacterium (*Serratia marcescens*) and that, consequently, our results were strongly influenced by the presence of the resident subspecies that posed the strongest resistance to the alien subspecies. These warrant some clarifications. First, Darwin's naturalization hypothesis relies on the presence of niche differences that tend to be smaller with increasing species relatedness. Given that bacterial subspecies propagate asexually (i.e., no crossing between subspecies) and may be ecologically distinct, and thus can often be considered equivalent to species (e.g., Hodgson et al. 2002; Brockhurst et al. 2007 [both studies reported on invasion experiments involving bacterial subspecies]), Darwin's hypothesis should apply equally to both subspecies and species levels. Indeed, our analyses showed that the resident and alien *S. marcescens* subspecies showed modestly different carbon usage patterns: 12 of the 95 carbon substrates on the Gram-negative Biolog plate can be used by one but not the other subspecies. Second, ob-

Table 2: Results of separate logistic regressions on invader establishment in the predation treatment

Source	df	χ^2	*P*	95% odds ratio confidence interval
Average phylogenetic distance	1	12.0949	.0005	>999.99, >999.99
Nearest phylogenetic distance	1	.0085	.9264	<.0001, >999.99
Resident species richness	1	.2832	.5946	.316, 1.936

served positive relationships between phylogenetic distance and invader abundance were largely driven by low invader abundances in communities containing the resident *S. marcescens* subspecies. This is analogous to the phenomenon that the presence of one or a few productive species, through the sampling effect, drives positive diversity-productivity relationships in experimental studies of biodiversity and ecosystem functioning (Cardinale et al. 2006). Also analogous to the sampling effect often considered as a valid biodiversity mechanism (e.g., Tilman et al. 1997; Jiang et al. 2008), the strong invasion resistance of communities containing the resident species with the shortest phylogenetic distance to the invader, largely responsible for the observed phylogenetic relatedness-invasion relationships, may also be considered a valid phylogenetic relatedness effect. Nevertheless, we recognize that phylogenetic distances between the invader and the other three resident species lie within a narrow range (0.309–0.398), making it difficult to assess the role of phylogenetic relatedness beyond that of the most closely related resident species. A recommendation for future experiments is thus to use species assemblages with more uniformly distributed phylogenetic distances between invading and resident species, which may likely be achieved with a larger resident species diversity gradient.

Our study provides the first experimental evidence that introduced species are less likely to establish self-sustaining populations and tend to attain smaller population sizes after successful establishment, in resident communities that are more closely phylogenetically related to the introduced species. While these findings clearly support Darwin's naturalization hypothesis, it is important to recognize that phylogenetic relatedness, in general, explained a modest fraction of variation in invasion success even in our highly simplified communities within relatively homogenous laboratory microcosms. We can think of at least two reasons for why this is the case. First, although phylogenetic niche conservatism was demonstrated, our choice of characterizing bacterial traits by their carbon usage patterns on Biolog plates means that potential differences in other aspects of species niche (e.g., the ability to cross feed) may have been overlooked. Under this possible scenario, phylogenetic relatedness between the invader and the resident species may not be a good indicator of their trait similarity and therefore strength of competition. Indeed, there is evidence for closely related species to be similar in some traits but differ in other traits (e.g., Cavender-Bares et al. 2004). Second, even if our characterization of phylogenetic niche conservatism was accurate, it may still not be straightforward to predict invasion success on the basis of pairwise phylogenetic distances alone, a surrogate of pairwise species interactions. This is because indirect interactions may arise in communities containing more than two species, resulting in profound indirect effects on species and communities that may not be readily predicted on the basis of pairwise interactions (Wootton 1994). Nevertheless, our results suggest that the phylogenetic distinctiveness of introduced species can be a useful factor to consider when predicting their potential success.

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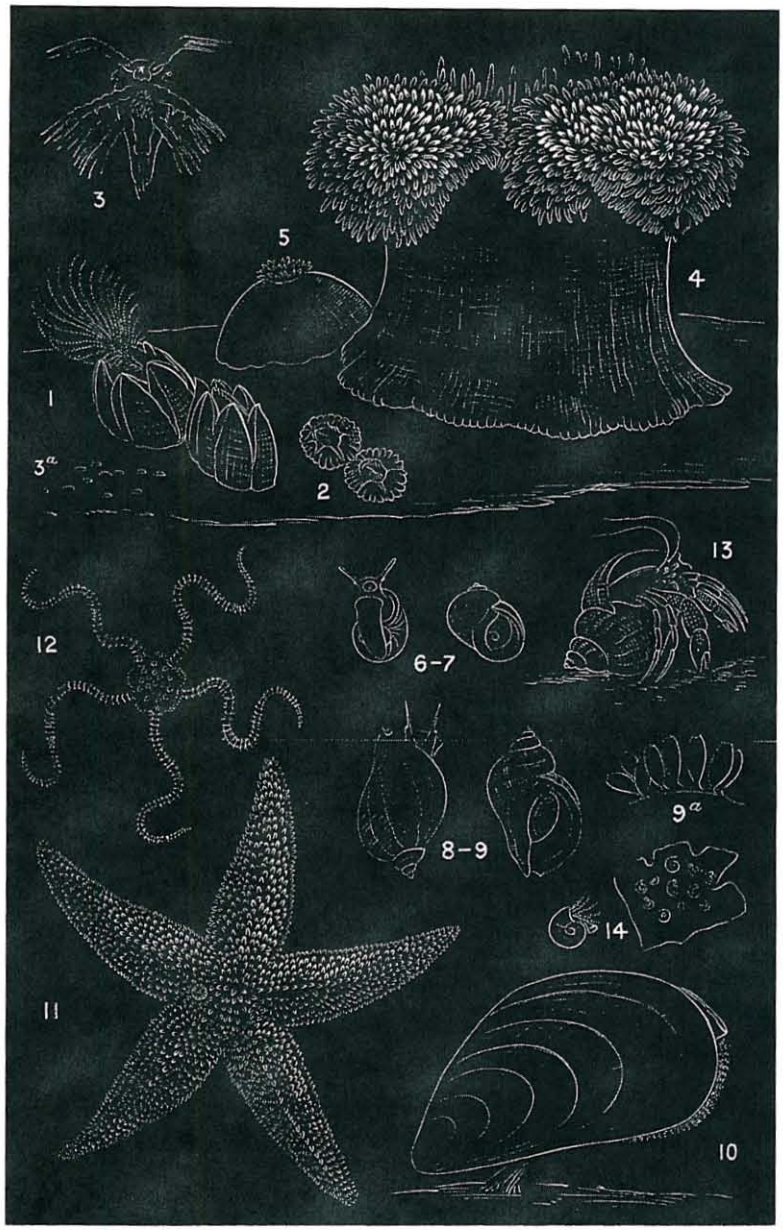

MORSE ON THE COMMON ANIMALS OF THE SEA-SHORE.

1, Common barnacles *Balanus eburneus* of Gould.; 2, *Balanus ovularis* of Gould.; 3, free-swimming young of barnacle; 3a, young barnacles directly after attachment; 4, sea anemone expanded *Metridium marginatum*; 5, sea anemone contracted; 6 and 7, periwinkle *Littorina palliata*; 8 and 9, cockle *Purpura lapillus*; 9a, egg cases of the same; 10, mussel *Mytilus edulis*; 11, starfish *Asterias vulgaris*; 12, brittle starfish *Ophiopholis bellis*; 13, hermit crab *Bernhardus longicarpus*; 14, *Spirorbis nautiloides*.